Self-organized patterns and traffic flow in colonies of organisms: from bacteria and social insects to vertebrates[*]

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Abstract

Flocks of birds and schools of fish are familiar examples of spatial patterns formed by living organisms. In contrast to the patterns on the skins of, say, zebra and giraffe, the patterns of our interest are *transient* although different patterns change over different time scales. The aesthetic beauty of these patterns have attracted the attentions of poets and philosophers for centuries. Scientists from

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various disciplines, however, are in search of common underlying principles that give rise to the transient patterns in colonies of organisms. Such patterns are observed not only in colonies of organisms as simple as single-cell bacteria, as interesting as social insects like ants and termites as well as in colonies of vertebrates as complex as birds and fish but also in human societies. In recent years, particularly over the last one decade, physicists have utilized the conceptual framework as well as the methodological toolbox of statistical mechanics to unravel the mystery of these patterns. In this article we present an overview emphasizing the common trends that rely on theoretical modelling of these systems using the so-called agent-based Lagrangian approach.

1 Introduction

In general, pattern is a general term for any recognizable regularity in the observed data. By "spatial" pattern we mean some kind of regularity in the arrangment of the constituents in space [1]. Similarly, when we monitor a time-dependent quantity over a period of time, any possible regularity in the temporal variation may be referred to as a "temporal" pattern [2, 3, 4]. Moreover, in phenomena where both spatial and temporal regularities occur simultaneously, a decoupling of the analysis of spatial and temporal patterns may not be possible and one has to deal with a spatio-temporal pattern [5].

Exotic patterns observed in living systems have attracted attention of physicists for a long time [6]. During the development of an organism, i.e., during the process of morphogenesis, cells are known to form specific patterns in tissues that form parts of specific organs or organ systems [7, 8, 9, 10]. However, in this paper we shall consider almost exclusively patterns exhibited by aggregates of organisms in their colonies [11]; schools of fish and flocks of migrating birds are, perhaps, the most familiar patterns of this type [12, 13]. The cellular patterns in tissues, after an initial transient period, remain practically unchanged for the remaining life period of the organism. In contrast, patterns exhibited by aggregates of organisms are transient; some of these aggregate are short-lived whereas others may persist for days.

Such aggregation is observed in colonies of organisms as simple as single-cell bacteria as well as in colonies of complex multi-cellular vertebrates. All types of locomotion, i.e., aerial, aquatic and terrestrial, of individual organisms can give rise to such aggregation. The popu-

lation of organisms in the aggregate may vary from tens to millions. These aggregates come in a wide range of shapes and sizes.

The reasons for the formation of such aggregates are now quite well understood. Individual organisms benefit (e.g., escaping predators) from aggregation despite some detrimental effects (e.g., getting infected by contagious disease). However, several fundamental questions regarding the structure and dynamics of these aggregates remain to be answered. For example, (a) what decides the shape of an aggregate and how do these form, (b) how does an aggregate maintain a shape over a period of time, (c) what triggers the changes of shapes of the aggregates, (d) how does fission and fusion of existing aggregates take place [14], etc.

Encouraged by the success of the conceptual framework of non-equilibrium statistical mechanics in the study of pattern formation in non-living systems [15, 16, 17], efforts have been made over the last decade to understand pattern formation in living systems by applying the same conceptual tools. It turns out that the aggregates of organisms exhibit richer patterns than those observed in non-living systems; this may be due to the fact that the constituent elements (i.e., the individual organisms) are living objects with many internal degrees of freedom. What makes these living organisms so different from their non-living counterparts is that each living object is an autonomous system that is capable of taking decision which is normally in its own self-interest. Thus, the evolution of the patterns involves a subtle interplay of the dynamical response of the individual organisms to their local surroundings and the global dynamics at the level of the colonies.

On the basis of the formation process, these aggregates can be broadly divided into two classes: (i) aggregates that "self-organize", and (ii) aggregates that form in response to external cues such as light or food. There are situations where an external cue nucleates an aggregate, but the aggregate soon grows in size dwarfing the original stimulus [18]. For example, a small school of fish may nucleate around some floating object, but soon the school may grow to such a huge size that the original attractant becomes irrelevant.

In the transient patterns exhibited by aggregates of organisms, one can identify two different characteristic time scales of dynamics: the shorter time scale is associated with the reflex and response of individual organisms to their immediate surroundings whereas the whole pattern changes on the longer time scale. In those patterns where

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terretrial locomotion drives each individual organisms and the pattern consists of long linear stretches, the spatio-temporal organization appears very similar to those in vehicular traffic. Perhaps, the most familiar examples are traffic of ants and termites on trails. In this article we shall also analyse such traffic flows from the perspective of statistical physics [20, 21, 22].

A common feature of most of the patterns considered in this paper is that each organism can be represented by a (self-propelled) particle and the system, as a whole, may be regarded as a collection of interacting (self-propelled) particles driven far from equilibrium [23]. The steady states of such systems are of current interest in non-equilibrium statistical mechanics [24, 25]. The transition from one such steady state to another, with the variation of parameters, is analogous to phase transitions exhibited by thermodynamic systems in equilibrium. The non-equilibrium phase transitions from one dynamical phase to another remain among the most challenging and least understood frontiers of statistical physics.

2 Theoretical approaches for modeling

The fundamental question to be addressed by any theory of patterns in colonies of organisms is the following: how do the *individual* decisions and *local* interactions of the individuals influence the *global* structure (shape, size, etc.), *collective* dynamics and function of the colony of the organisms? What is the interplay of deterministic and stochastic dynamics?

2.1 Different types of theoretical approaches

First of all, the theoretical approaches can be broadly divided into two categories: (I) "Eulerian" and (II) "Lagrangian". In the *Eulerian* models individual organisms do not appear explicitly and, instead, one considers only the population densities (i.e., number of individual organisms per unit area or per unit volume). But, the *Lagrangian* models describe the dynamics of the individual organisms explicitly. Just as "microscopic" models of matter are formulated in terms of molecular constituents, the Lagrangian models of pattern are also developed in

terms of the constituent organisms. Therefore, the Lagrangian models are often referred to as "microscopic" models.

In the recent years, it has been emphasized by several groups (see, for example, ref. [26]) that although the patterns of the colonies are manifest only at the level of the population, the patterns are emergent collective properties that are determined by the responses of the individuals to their local environments and the local interactions among the individual organisms. Therefore, in order to gain a deep understanding of the pattern formation process, it is essential to investigate the linkages between these two levels of biological organization.

Usually, but not necessarily, space and time are treated as continua in the Eulerian models and partial differential equations (PDEs) or integro-differential equations are written down for the time-dependent local collective densities of the organisms [27, 28, 29]. The Lagrangian models have been formulated following both continuum and discrete approaches. In the continuum formulation of the Lagrangian models, differential equations describe the individual trajectories of the organisms [26].

For developing Lagrangian model, one must first specify the *state* of each individual organism. The informations which may be needed for the complete specification of the state include, for example, the location (position in space whose dimensionality may be one, two or three), genotype and phenotype, ontogenetic status (age, size and maturity), physiological status (hunger), behavioral status (motivation), etc. [26]. In addition, the environmental informations must also be provided; these may include physical and chemical features of the environment, resources in the environment, etc. The dynamical laws governing the time-evolution of the system must predict the state of the system at a time $t + \Delta t$, given the corresponding state at time t. The change of state should reflect the response of the system in terms of movement of the individual organisms, their mortality, reproduction (and consequent population growth).

A natural framework for the mathematical formulation of such models is the Newton's equations for individual organisms; each organism is modelled as a "particle" subjected to some "effective forces" arising out of its interaction with the other organisms in the colony [30, 31]. These forces not only cause their movements but also their alignments. In addition, the organisms may also experience viscous drag and some random forces ("noise") that may be caused by the surrounding fluid medium. Even in the absence of any direct phys-

ical interaction between the organisms (other than the "hard-core" repulsion) there may be some other "effective interactions" which are often referred to as "social" interactions. Some of these interactions capture the effects of communications via chemical signalling; these include, for example, communications among amoeba forming a multicellular slug or those between ants on a trail. This type of models are sometimes formulated in terms of an effective energy landscape. Each organism executes moves in its own energy landscape which, in turn, varies with time because of the movement of the other organisms [32]. In contrast to the forces arising from physical interactions, the social forces do not necessarily obey Newton's third law! In this paper we shall present an explicit example for such social interactions in the context of the pedestrian dynamics.

Most of the recent Lagrangian models, however, have been formulated on discretized space and the temporal evolution of the system in discrete time steps are prescribed as dynamical update rules using the language of cellular automata (CA) [33, 34] or lattice gas (LG) [35]. Since each of the individual organisms may be regarded as an agent, the CA and LG models are someties also referred to as agent-based models [36].

One advantage of the continuum models is that all the tools for analytical treatment of differential- and integro-differential equations are readily available [37, 38]. However, a continuum formulation is usually sensible only for large and *dense* aggregates but hard to justify for loosely packed aggregates. Moreover, even if a continuum description can be justified, what is even harder to justify is the analytical form of the inter-organism interactions, which are required for writing down the equations of motion for the individual organisms in the Lagrangian approach. Furthermore, the differential equations often turn out to be too complicated to be solved analytically. Numerical solution of these equations require discretization of both space and time. Therefore, the alternative discrete formulations, based on CA and LG, may be used from the beginning [39].

In fact, there are some further advantages in modeling biological systems with CA and LG. Biologically, it is quite realistic to think in terms of the way each individual organism responds to its local environment and the series of actions they perform. The lack of detailed knowledge of these behavioral responses is compensated by the rules of CA. Usually, it is much easier to devise a reasonable set of logic-based rules, instead of cooking up some effective force for dynamical

equations, to capture the behaviour of living organisms. Moreover, because of the high speed of simulations of CA and LG, a wide range of possibilities can be explored which would be impossible with more traditional methods based on differential equations. Furthermore, it may be possible to derive continuum Eulerian models by appropriately coarse-graining agent-based Lagrangian models under some justifiable approximations.

The most satisfactory and convenient *analytical* approach may be to use a hybrid of the Lagragian-Eulerian methods. One can start with a agent-based microscopic model following the Lagrangian approach and, then, derive corresponding macroscopic Eulerian models from these equations under reasonable approximations. It may be possible to solve the approximate Eulerian equations using the analytical tools for solving PDEs.

2.2   Types of ordering in the aggregate

The aggregates formed by the organisms can exhibit different types of ordered structures depending on the individual and/or collective features as well as external environmental conditions.

Some aggregates are compact Euclidean objects while others exhibit fractal structure. Among the compact patterns, several different types of ordering have been observed. For example, the positions and orientations of the individual organisms may correspond to those of non-spherical molecules in a crystal. However, most often, the positions of the organisms do not form a regular lattice but they are all oriented more or less in the same direction; some of this type of structures of the aggregates are analogues of nematic liquid crystals [40]. In some other aggregates like, for example, swarms of mosquitoes, there is no spatial or orientational ordering inside the aggregate although the aggregate persists.

It has been realized for quite some time that, in reality, swarms have a finite size. Therefore, attempts should be made to obtain *localized* patterns [41] or propagating *bands* [38], rather than propagating surfaces, to capture migrating *finite* colonies.

3 Patterns of aggregates of cells and uni-cellular organisms

Various species of uni-cellular organisms, e.g., bacteria, amoeba, etc., form aggregates with wide varieties of patterns. Moreover, some types of cells, which normally form parts of multi-cellular organisms, are also capable of forming interesting patterns when these are isolated from the organism and grown in cultures.

3.1 Patterns of bacterial colonies in biofilms

The microbial biofilms pose not only intellectual challenge to physicists interested in the patterns of bacterial colonies but also of practical interest in microbiology. For example, the dental plaques, the bacterial films formed inside water pipes, etc. are examples of microbial biofilms. The growth of such structures have been invesigated using CA approaches [42].

Normally, in the laboratory, bacterial colonies are grown on substrates with a high nutrient level and intermediate agar concentration. Patterns of the aggregates formed in colonies grown in such comfortable conditions are compact. However, harsh conditions for bacterial colonies can be created, for example, by using low level of nutrients; aggregates of bacteria formed in such environments can be very complex and interesting from the point of view of pattern formation [43, 44]. Hydrodynamics is also likely to play some role in the growth of the bacterial colonies in wet conditions [45].

The colonies of *Proteus mirabilis* form circular swarms that have a terrace-like structure. Modeling such swarms have been attempted so far following, to our knowledge, only Euclidean approach [46, 47]. Very recently, Indekeu and Giuraniuc [48] have developed a CA model of "nutrient-limited aggregation" and growth of bacterial towers. The three-dimensional system is modeled as a simple cubic lattice where each site can be either empty or occupied by a bacterium or nutrient or water. Chemotaxis, rather than diffusion, drives the growth process.

There are speculations as to the potential applications of the new understanding of the mechanisms of pattern formation in bacterial colonies to synthesize systems, which are too complicated to produce by conventional methods, through self-organization [49].

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3.2 Patterns of aggregates of amoeba; slime molds

The slime mold Dictyostelium discoideum can exist in two different forms, namely, either as a population of individual amoeba or as a multi-cellular organism consisting of thousands of cells [50, 51]. These amoeba feed on other bacteria and can exist as a well dispersed colony of uncorrelated individual organisms when the supply of nutrients is abundant. However, when nutrients become scarce, the amoeba begin a collective restructuring of the colony through communication via chemical signalling. The colony exhibits a sequence of different spatial patterns; the final three-dimensional structure is a fruit body that looks similar to a small mushroom with very large number of spores. The spores get spread out over a large area by wind. When these land in areas with sufficiently high supply of nutrients, they give rise to a new well dispersed population of amoeba.

From the perspective of transient patterns, the intermediate stages of aggregation of the amoeba are most interesting. The initial patterns consist of concentric rings which gradually transform to rotating spirals. At a later stage, the slow movements of the cells towards the centers of such patterns transform the patterns themselves into a system of thin dense streaks.

The aggregation of the amoeba Dictyostelium discoideum was modelled long ago (for example, by Keller and Segel [52]) using an Eulerian approach (see also ref.[53] for the recent literature on theoretical models). Kessler and Levin [54] have developed a discrete CA-type model to study these spatial patterns. Each cell was represented by a two-state automaton (a "bion") which is capable of measuring the concentration and concentration gradients of cAMP as well as sense the presence of nearby bions.

In the Kessler-Levin model [54], initially, a random fraction of the sites (typically 5-20 percent) of a square lattice are occupied by the bions. In addition, cAMP concentration c was assumed to obey a discretized diffusion equation on the lattice. Each bion remains in the state 0 until it detects a local concentration above a predetermined threshold. As soon as the local cAMP concentration exceeds the threshold, the bion makes a transition to the state 1 and emits an amout Δc of cAMP over the next τ time steps. Then the bion remains in a quiescent state 2 for the next t_R time steps before reverting back to the state 0; in the quiescent state the bion remains immune

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to further excitation.

The rule for the movement of the individual cells in the Kessler-Levine model [54] is as follows: for a cell located, at a given time step t, at the lattice site i, j, the discretized gradients in the concentrations c of cAMP are computed using

$$(\nabla c)_x = (c_{i+1,j}^{(t)} - c_{i-1,j}^{(t)})/2$$

$$(\nabla c)_y = (c_{i,j+1}^{(t)} - c_{i,j-1}^{(t)})/2$$

If the cell is in the excited state 1 and if at least one of the two gradients exceeds the predetermined threshold, the cell attempts to move to the next neighbouring lattice site with the higher concentration of cAMP in that direction. If gradients in both the directions exceed the threshold, the cell attempts to move in the direction determined by the diagonal in between those two directions of increasing cAMP concentration. However, the attempt of hopping is successful only if the target site is not occupied by any other cell. Each cell can move only once in each excitation cycle. Carrying out computer simulations of this model, Kessler and Levin [54] observed the spiral spatial patterns characteristic of the aggregation during the formation of the multicellular slug. A more detailed CA model, which is intended to account for the patterns at different stages of evolution, has been developed more recently by Savill and Hogeweg [55].

3.3 Patterns in colonies of myxobacteria

Myxobacteria form large clusters and move like a pack of wolves. Each individual myxobacterium preys on several other microorganisms. In contrast to communication system based on the diffusible morphogens in Dictyostelium discoideum, the myxobacteria use an altogether different mechanism of communication where cells communicate with each other by direct physical contact. Periodic waves of movements, called ripples, have been observed in these colonies. However, in spite of superficial similarities, there are crucial differences in the properties of these ripples and similar patterns observed in cellular slime mold Dictyostelium discoideum. In particular, the colliding wave fronts in case of Dictyostelium discoideum annihilate each other whereas the waves in the colonies of myxobacteria can pass through each other. This phenomenon has been reproduced by a model [56], formulated in the spirit of Lagragian approach, where the trajectories of the individual myxobacteria are described by a set of Langevin-like equations.

3.4 Pattern of aggregates of fibroblasts

Fibroblasts are a special type of cells found in connective tissues. In the laboratory these cells can be extracted from their natural locations and their in-vitro aggregation can be studied using cultures on a petri dish. The two-dimensional colonies of such cells have been found to form patches where each patch consists of a single layer of hundreds of fibroblasts with a single axis of orientation. The competing contiguous patches eventually merge into a large array with one single axis of orientation.

A CA model for this pattern formation by fibroblasts was developed by Edelstein-Keshet and Ermentrout [57]. Each of the lattice sites could be either empty or occupied by a cell. Each cell is assigned an *orientation* and *a state of binding*. The orientation of a cell can be denoted by an arrow; the direction of the arrow determines the direction of the movement of the cell in the next time step. The state of binding (i.e., whether or not the cell is bound to an aggregate) determines whether or not it is allowed to move. However, both the orientation and the state of binding are dynamic variables that can change with time.

On a discrete lattice, however, the arrow can point in only a finite set of discrete directions. For example, implementing the model on a square lattice, Edelshtein-Keshet and Ermentrout [57] allowed the arrow to be pointed towards any of eight neighbouring sites surrounding it (i.e., the four nearest-neighbour as well as the four next nearest-neibour sites). Consequently, each cell could change its orientation by an angle that would be an integral multiple of $45°$. For the sake of simplicity, only two discrete states of binding are assumed; the cell is either bound to an aggregate or unbound (i.e., not part of any aggregate). Therefore, the total number of possible states of each cell is twelve while that of each lattice site is thirteen.

Starting from a homogeneous state with random orientations, the state of the system is updated at each discrete time step according to the following rules:

(i) an unbound cell reorients by one angular unit (e.g., 45^0 on a square lattice) with probability p_0,

(ii) an unbound cell may reverse its motion with probability p_R,

(iii) if an unbound cell comes in contact with another cell or group of cells, the probabilty of binding and aligning is p_A if the angle of contact is small enough; otherwise the approaching cell reverses its

direction and moves away,

(iv) bound cells do not move; the probability that a bound cell detaches from a group is p_D.

By carrying out computer simulations, Edelstein-Keshet and Ermentrout [57] demonstrated that this simple model captures the essential qualitative features of the aggregation process observed in the in-vitro experiments.

4 Patterns in social insect colonies

From now onwards, in this paper we shall study patterns of the aggregates formed by multi-cellular organisms. We begin with the simpler (and smaller) organisms and, then, consider those of organisms with larger sizes and more complex physiology.

Termites, ants, bees and wasps are the most common social insects, although the extent of social behavior, as compared to solitary life, varies from one sub-species to another [58]. The ability of the social insect colonies to function without a leader has attracted the attention of experts from different disciplines [59, 60, 61, 62, 63, 64, 65, 66]. Insights gained from the modeling of the colonies of such insects are finding important applications in computer science (useful optimization and control algorithms) [67], communication engineering [68], artificial "swarm intelligence" [69] and micro-robotics [70] as well as in management [71].

4.1 Ant-trail formation

Ants communicate with each other by dropping a chemical (generically called *pheromone*) on the substrate as they move forward [58, 18, 19]. Although we cannot smell it, the trail pheromone sticks to the substrate long enough for the other following sniffing ants to pick up its smell and follow the trail. This process is called *chemotaxis* [43].

Rauch et al.[32] developed a continuum model, following a hybrid of the Lagrangian and the Eulerian approaches in terms of an effective energy landscape. They wrote one set of stochastic differential equations for the positions of the ants and another set of PDEs for the local densities of pheromone.

Suppose a set of "particles", each of which represents an ant, move in a potential field $U[\sigma(x)]$, where the potential at any arbitrary lo-

cation x is determined by the local density $\sigma(x)$ of the pheromone field. Consequently, each "particle" experiences an "inertial" force $\vec{F}(x) = -\nabla U(x)$. Each "particle" is also assumed to be subjected to a "frictional force" where "friction" merely parametrizes the tendency of an ant to continue in a given direction: a smaller "friction" implies that the ant's velocity persists for a longer time in a given direction. The equation of motion for the "particles" (stochastic differential equation) are assumed to have the form [32]

$$\ddot{x} = -\gamma \dot{x} - \nabla U[\sigma(x)] + \eta(t) \tag{1}$$

where $\eta(t)$ is a Gaussian white noise with the statistical properties

$$\langle \eta(t) \rangle = 0 \tag{2}$$

and

$$\langle \eta(t)\eta(t') \rangle = \frac{1}{\beta}\delta(t - t') \tag{3}$$

The strength $1/\beta$ of the noise determines the degree of determinacy with which the particle would follow the gradient of the local potential; the larger the value of β the stronger is the tendency of the particle to follow the potential gradient.

Thus, the movement of an ant may be described as the noisy motion of a particle in an "energy landscape". However, this energy landscape is not static but evolves in response to the motion of the particle as each particle drops pheromone at its own location at a rate g per unit time. Assuming that pheromone can diffuse in space with a diffusion constant D and evaporate at a rate κ, the equation governing the pheromone field is given by

$$\frac{\partial \sigma(x)}{\partial t} = D\nabla\sigma(x) + g\rho(x) - \kappa\sigma(x) \tag{4}$$

where $\rho(x)$ is the local density of the particles at x. Finally, Rauch et al. assumed that the function $U[\sigma(x)]$ has the form

$$U[\sigma(x)] = -\ln\left(1 + \frac{\sigma}{1 + \delta\sigma}\right) \tag{5}$$

where $1/\delta$ is called the capacity.

Watmough and Edelstein-Keshet [72] introduced a CA model to study the formation of ant-trail networks by foraging ants. In this model, each ant is described by its discrete position and velocity on

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a discrete. The rules for updating the positions and velocities of the ants as well as the pheromone contration on the trail are as follows:

(i) The ants move at a fixed speed; if the ant is a forager and not following a trail, its movements are random.

(ii) Each ant deposits a trail pheromone at a constant rate as it moves.

(iii) The trail pheromone also evaporates at a constant rate.

(iv) The probability $p_\ell(c)$ per unit time that an ant will keep following a trail (and not loose the trail) is a function of the local pheromone concentration; the function $p_\ell(c)$ is to be specified separately.

(v) When an ant, following a trail, reaches a point of bifurcation it chooses one of the two branches where the rule for choosing the branch is prescribed in the beginning.

Carrying out computer simulations of this CA model, Watmough and Edelstein-Keshet [72] observed trail patterns that look very similar to real ant-trail networks. The formation of human trails have some similarities with that of ant-trails; some recent models that elucidate the mechanisms of the emergence of human trails will be discussed later in this article.

4.2   Phase transition between disordered and ordered foraging

Beekman et al. [73] pointed out close similarities between phase transitions in non-living systems and that of foraging behaviour on the ant-trail.

A foraging ant that discovers a food source lays down a pheromone trail as it crawls back to its nest. But, the trail would completely disappear unless it is reinforced by other ants before the original pheromone, a volatile chemical, evaporates away. From the study of their model, Beekman et al. [73] found that the two important relevant parameters are (a) the total number of ants within the colony, and (b) the individual rate at which the ants discover food sources. They showed that (i) when the independent discoveries of food sources are infrequent, a first order (discontinuous) phase transition from a disordered foraging behaviour (i.e., foraging without a pheromone trail) to ordered foraging (i.e., trail-based foraging) takes place as the size of the colony increses; (ii) this transition exhibits hysteresis (i.e., history-dependence): when the rate of individual discoveries of food sources decreases the system chooses one of the two alternative modes

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of behaviour- either no trail or a well used trail- depending on the initial conditions. In other words, when the independent discoveries of food sources become infrequent, the colonies find it difficult to start a trail but can still sustain an existing trail.

4.3 Traffic on ant-trails

In [74, 75, 76] we have developed particle-hopping models, formulated in terms of a stochastic cellular automaton (CA) (or, lattice gas), which may be interpreted as models of uni-directional and bi-directional traffic flow in an ant-trail. These models are not intended to address the question of the emergence of the ant-trail [77], but focus on the traffic of ants on a trail which has already been formed. The model generalizes the totally asymmetric simple exclusion process (TASEP) [78, 79, 25] with parallel dynamics by taking into account the effect of the pheromone.

In our model of uni-directional ant-traffic the ants move according to a rule which is essentially an extension of the TASEP dynamics. In addition, a second field is introduced which models the presence or absence of pheromones (see Fig. 1). The hopping probability of the ants is now modified by the presence of pheromones. It is larger if a pheromone is present at the destination site. Furthermore, the dynamics of the pheromones has to be specified. They are created by ants and free pheromones evaporate with probability f per unit time. Assuming periodic boundary conditions, the state of the system is updated at each time step in two stages (see Fig. 1). In stage I ants are allowed to move while in stage II the pheromones are allowed to evaporate. In each stage the *stochastic* dynamical rules are applied in parallel to all ants and pheromones, respectively.

Stage I: Motion of ants

An ant in a site cannot move if the site immediately in front of it is also occupied by another ant. However, when this site is not occupied by any other ant, the probability of its forward movement to the ant-free site is Q or q, depending on whether or not the target site contains pheromone. Thus, q (or Q) would be the average speed of a *free* ant in the absence (or presence) of pheromone. To be consistent with real ant-trails, we assume $q < Q$, as presence of pheromone increases the average speed.

Stage II: Evaporation of pheromones

Trail pheromone is volatile. So, pheromone secreted by an ant will gradually decay unless reinforced by the following ants. In order to capture this process, we assume that each site occupied by an ant at the end of stage I also contains pheromone. On the other hand, pheromone in any 'ant-free' site is allowed to evaporate; this evaporation is also assumed to be a random process that takes place at an average rate of f per unit time.

The total amount of pheromone on the trail can fluctuate although the total number N of the ants is constant because of the periodic boundary conditions. In the two special cases $f = 0$ and $f = 1$ the stationary state of the model becomes identical to that of the TASEP with hopping probability Q and q, respectively.

One interesting phenomenon observed in the simulations is coarsening. At intermediate time usually several non-compact clusters are formed (Fig. 2(a)). However, the velocity of a cluster depends on the distance to the next cluster ahead. Obviously, the probability that the pheromone created by the last ant of the previous cluster survives decreases with increasing distance. Therefore clusters with a small headway move faster than those with a large headway. This induces a coarsening process such that after long times only one non-compact cluster survives (Fig. 2(b)). A similar behaviour has been observed also in the bus-route model [80, 81].

In vehicular traffic, usually, the inter-vehicle interactions tend to hinder each other's motion so that the average speed of the vehicles decreases *monotonically* with increasing density. In contrast, in our model of uni-directional ant-traffic the average speed of the ants varies *non-monotonically* with their density over a wide range of small values of f because of the coupling of their dynamics with that of the pheromone. This uncommon variation of the average speed gives rise to the unusual dependence of the flux on the density of the ants in our uni-directional ant-traffic model. Furthermore, the flux is no longer particle-hole symmetric.

It is possible to extend the model of uni-directional ant-traffic to a minimal model of bi-directional ant-traffic [76]. In the models of bi-directional ant-traffic the trail consists of *two* lanes of sites. These two lanes need not be physically separate rigid lanes in real space. In the initial configuration, a randomly selected subset of the ants move in the clockwise direction in one lane while the others move

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counterclockwise in the other lane. The numbers of ants moving in the clockwise direction and counterclockwise in their respective lanes are fixed, i.e. ants are allowed neither to take U-turn[1] nor to change lane.

The rules governing the dropping and evaporation of pheromone in the model of bi-directional ant-traffic are identical to those in the model of uni-directional traffic. The *common* pheromone trail is created and reinforced by both the outbound and nestbound ants. The probabilities of forward movement of the ants in the model of bi-directional ant-traffic are also natural extensions of the similar situations in the uni-directional traffic. When an ant (in either of the two lanes) *does not* face any other ant approaching it from the opposite direction the likelihood of its forward movement onto the ant-free site immediately in front of it is Q or q, respectively, depending on whether or not it finds pheromone ahead. Finally, if an ant finds another oncoming ant just in front of it, as shown in Fig. 3, it moves forward onto the next site with probability K.

Since ants do not segregate in perfectly well defined lanes, head-on encounters of oppositely moving individuals occur quite often although the frequency of such encounters and the lane discipline varies from one species of ants to another. In reality, two ants approaching each other feel the hindrance, turn by a small angle to avoid head-on collision [83] and, eventually, pass each other. At first sight, it may appear that the ants in our model follow perfect lane discipline and, hence, unrealistic. However, that is not true. The violation of lane discipline and head-on encounters of oppositely moving ants is captured, effectively, in an indirect manner by assuming $K < Q$. But, a left-moving (right-moving) ant *cannot* overtake another left-moving (right-moving) ant immediately in front of it in the same lane. It is worth mentioning that even in the limit $K = Q$ the traffic dynamics on the two lanes would remain coupled because the pheromone dropped by the outbound ants also influence the nestbound ants and vice versa.

Fig. 4 shows fundamental diagrams for the two relevant cases $q < K < Q$ and $K < q < Q$ and different values of the evaporation probability f for equal densities on both lanes. In both cases the unusual behaviour related to a non-monotonic variation of the average speed with density as in the uni-directional model can be observed [76].

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[1]U-turns of so-called followers on pre-existing trails are very rare [82].

An additional feature of the fundamental diagram in the bi-directional ant-traffic model is the occurrence of a plateau region. This plateau formation is more pronounced in the case $K < q < Q$ than for $q < K < Q$ since they appear for all values of f. Similar plateaus have been observed earlier [84, 85] in models related to vehicular traffic where randomly placed bottlenecks slow down the traffic in certain locations along the route.

The experimental data available at present [86, 87] are not accurate enough to test the predictions mentioned above. More accurate measurements, using novel methodologies are in progress [88].

5   Patterns in the colonies of vertebrates

Migrating fish schools and bird flocks have one common feature that both of these correspond to a non-vanishing average linear drift velocity. In theoretical models a bird or a fish can be represented by a *polar* self-propelled particle. The nature of the dynamical phases and phase transitions of both polar and *apolar* self-propelled particles have been investigated extensively in the literature over the last decade [89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99].

Ramaswamy and collaborators [100] have studied the hydrodynamic fluctuations of liquid-crystal-like ordered dynamical phases of self-propelled apolar particles. Carrying out linear stability analysis, they have not only predicted certain long-wavelength instabilities but also indicated the possibility of novel propagating modes which, in principle, may be observed in experiments with real or artificial self-propelled particles.

The structure and function of schools of fish have attracted attention for the last few dacades [101, 102]. But, serious efforts have been only over the last few years [103, 104] in the understanding the mechanism of their formation through self-organization in terms of quantitative models. For example, Niwa [105] has developed a model of fish schooling following the Lagrangian approach. However, the equations describing the movements of the individual fishes are written in terms of continuous space and time; in fact, these equations are very similar to Langevin equations for Brownian particles subjected to not only intertial forces but also viscous drag and random noise.

Stöcker [106] has developed a CA model for tuna school formation. However, for the sake of simplicity, we outline here the main idead

behind the first CA model of fish schooling, developed by Huth and Wissel [107]. Each fish is characterized by its position and velocity vectors. Suppose, r_{ij} denotes the magnitude of the separation between the fish labelled by the integer indices i and j. In order to decide the position and velocity of the fish i, one needs to draw three imaginary spheres of radii r_1, r_2 and r_3 ($r_1 < r_2 < r_3$) around it. If the fish j is located within the smallest sphere, then it would have a repulsive effect on the fish i such that the fish i will have a tendency to swim away in a direction perpendicular to the direction of the velocity of the fish j. On the other hand, if the fish j is located anywhere within the distance $r_1 < r_{ij} < r_2$, the fish i will tend to move parallel to the velocity of the fish j. In case $r_2 < r_{ij} < r_3$, the fish i will be attracted towards the fish j. Finally, if the fish j is located outside the largest sphere of radius r_3, i.e., $r_{ij} > r_3$, it will have no influence on the movement of the fish i. Huth and Wissel [107] also introduced rules for combining the influences of more than one fish within the spheres of influence.

6 Human traffic on trails

Various kinds of pattern formation can also be observed in human societies, especially in pedestrian dynamics [108]. As we will see, the human "intelligence" plays only a minor role. Instead, the observed effects can be understood as simply collective phenomena in systems of interacting particles. In fact, some effects (like lane formation) also appear in true physical systems [109]. Before we present a CA model that reproduces the essentials of pedestrian dynamics we list some of the observed collective phenomena.

6.1 Collective phenomena and pattern formation

One of the reasons why the investigation of pedestrian dynamics is attractive for physicists is that many interesting collective effects and self-organization phenomena can be observed [108, 21].

Jamming: At large densities various kinds of jamming phenomena occur, typically at bottlenecks like doors or narrowing corridors. This kind of clogging effect does not depend strongly on the microscopic dynamics of the particles. Other types of jamming occur in the case

of counterflow where two groups of pedestrians mutually block each other. This happens typically at high densities and when it is not possible to turn around and move back, e.g. when the flow of people is large.

Lane formation: In counterflow with groups of people moving in opposite directions, a kind of spontaneous symmetry breaking occurs (see Fig. 5). The motion of the pedestrians can self-organize into dynamically varying lanes where people move in just one direction [110]. Thus, strong interactions with oncoming pedestrians are reduced and a higher walking speed is possible.

Oscillations: In counterflow at bottlenecks, e.g. doors, oscillatory changes of the direction of motion are observed. Once a pedestrian is able to pass the bottleneck it becomes easier for others to follow her/him in the same direction until somebody is able to pass (e.g. through a fluctuation) the bottleneck in the opposite direction (see Fig. 6).

Patterns at intersections: At intersections various collective patterns of motion can be formed. A typical example are short-lived roundabouts which make the motion more efficient. Even if these are connected with small detours the formation of these patterns can be favourable since they allow for a "smoother" motion.

Panics: In panic situations, many counter-intuitive phenomena can occur. In the faster-is-slower effect [111] a higher desired velocity leads to a slower movement of a large crowd. Typical is also herding behaviour where people just blindly follow others. Such effects are extremely important for evacuations in emergency situations.

6.2   Modelling Pedestrian Dynamics

Several different types of models have been suggested in order to reproduce and understand the phenomena described in the previous subsection. In addition, practical applications, e.g. in the planning of public buildings like football stadiums, are of considerable importance. The latter requires models that can simulate even large crowds efficiently but, at the same time, are realistic enough to capture the essential aspects of the dynamics, e.g. the observed collective effects. Therefore it is not surprising that only a few models are able to achieve this.

A continuum approach that has been very successful in modelling pedestrian dynamics, is the so-called social force model (see e.g. [21,

110] and references therein). Pedestrians are treated as particles subject to long-ranged forces induced by the social behaviour of the individuals. The typical structure of the force between the pedestrian is described by [111]

$$\mathbf{f}_{ij} = \mathbf{f}_{ij}^{(soc)} + \mathbf{f}_{ij}^{(phys)}. \tag{6}$$

Here $\mathbf{f}_{ij}^{(phys)}$ is a physical force and describes friction and compression when pedestrians make contact. $\mathbf{f}_{ij}^{(soc)}$ is a repulsive social force modelling the tendency to keep a certain distance to other individuals. Typically it is long-ranged and has the form

$$\mathbf{f}_{ij}^{(soc)} = A_i g_{ij}(\lambda_i, \varphi_{ij}) \exp\left(r_{ij}/\xi_i\right) \mathbf{n}_{ij} \tag{7}$$

where r_{ij} is (a suitably defined) distance between the pedestrians and $\mathbf{n}_{ij}$ a normalized vector pointing from individual j to i. Apart from the interaction strength A_i and the range ξ_i of the force it has also a direction dependence that enters through the function g_{ij} which depends on a parameter λ_i controlling the anisotropy of interactions and the angle φ_{ij} between the directions of motion.

This idea leads then to equations of motion similar to Newtonian mechanics. There are, however, important differences since, e.g., in general the third law ("action = reaction") is not fulfilled by social forces.

So-called active-walker models [77, 115] have been used to describe the formation of human or animal trails etc. Here the walker leaves a trace by modifying the underground on his path. This modification is similar to chemotaxis since it can be regarded as a stimulus for other pedestrians. Vegetation is destroyed by the walker and so it becomes more attractive for others to follow the same path.

Most cellular automata (CA) models for pedestrian dynamics proposed so far are rather simple [116, 117, 118, 119] and can be considered as generalizations of the Biham-Middleton-Levine model for city traffic [120]. However, these models are not able to reproduce all the collective effects observed empirically.

In the following we present the so-called floor field CA model developed in [112, 113, 114]. It is a CA with stochastic dynamics and in many respects can be regarded as a two-dimensional version of the ant trail model of Sec. 4.3. The basic idea is to model interactions between pedestrians as a kind of virtual chemotaxis. Like an ant on a ant trail any *moving* pedestrian creates a *virtual* trace that influences the motion of other pedestrians by enhancing the probability of

motion in the same direction. In this way long-ranged spatial interactions are translated into local interactions, but with "memory". This reduces the number of interaction terms considerably (from $O(N^2)$ to $O(N)$ for crowds of N people) and allows for a much more efficient implementation on a computer.

The idea of a virtual trace can be generalized to a so-called *floor field*. This floor field includes the virtual trace created by the pedestrians as well as a static component which does not change with time. The latter allows to model e.g. preferred areas, walls and other obstacles. The pedestrians then react to both types of floor fields. The 'particles' in the model have very little "intelligence" and the formation of complex structures and collective effects is solely achieved through self-organization. No detailed assumptions about the human behaviour are necessary.

As already emphasized, it is similar to a 2-dimensional variant of the ant trail model. We have a hard-core exclusion so that each cell can be occupied at most by one pedestrian. In contrast to pheromone field in the ant trail model, the floor fields are virtual and, therefore, not restricted by hard-core exclusion. Here we do not give a complete definition of the model here which can be found in [112, 113, 114].

These basic principles are already sufficient to reproduce the effects described in Sec. 6.1, such as lane formation in a corridor, herding and oscillations at a bottleneck [112, 113]. In addition, the model can also be used very efficiently for the simulation of emergency situations [121].

7 Conclusion

Aesthetically beautiful patterns are formed by aggregates of living organisms. Such patterns are formed by organisms as simple as unicellular bacteria, by social insects like ants and termites as well as by more complex vertebrates like birds and fish. All the patterns of our interest are transient in nature. Interesting transient patterns emerge also in human societies. During time intervals that are short compared to the lifetime of a pattern formed by the terrestrial locomotion of organisms, the collective movements on linear segments often appear similar to vehicular traffic. In this article we have presented a critical review of the theoretical works, particularly those published over the last decade, focussing almost exclusively on the agent-based models

formulated in the spirit of the classical Lagrangian approach. These include the Langevin-like stochastic differential equations, where dynamics is formulated in continuous space-time to describe the trajectories of the individual organisms. Another class of agent-based discrete models are developed using the language of cellular-automata where the dynamics is formulated in terms of update rules. Direct comparison with controlled experiments have been possible mostly in case of micro-organisms and small insects. The challenge is to unveil the mystery of these transient tapestry and traffic of life.

Acknowledgements

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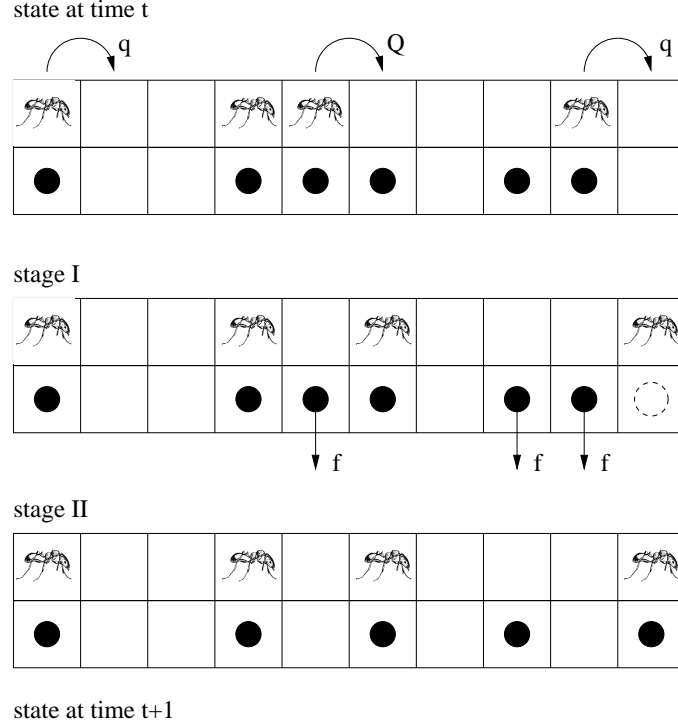
state at time t

stage I

stage II

state at time t+1

Figure 1: Schematic representation of typical configurations of the unidirectional ant-traffic model. The symbols • indicate the presence of pheromone. This figure also illustrates the update procedure. Top: Configuration at time t, i.e. *before stage I* of the update. The non-vanishing probabilities of forward movement of the ants are also shown explicitly. Middle: Configuration *after* one possible realisation of *stage I*. Two ants have moved compared to the top part of the figure. The open circle with dashed boundary indicates the location where pheromone will be dropped by the corresponding ant at *stage II* of the update scheme. Also indicated are the existing pheromones that may evaporate in *stage II* of the updating, together with the average rate of evaporation. Bottom: Configuration *after* one possible realization of *stage II*. Two drops of pheromones have evaporated and pheromones have been dropped/reinforced at the current locations of the ants.
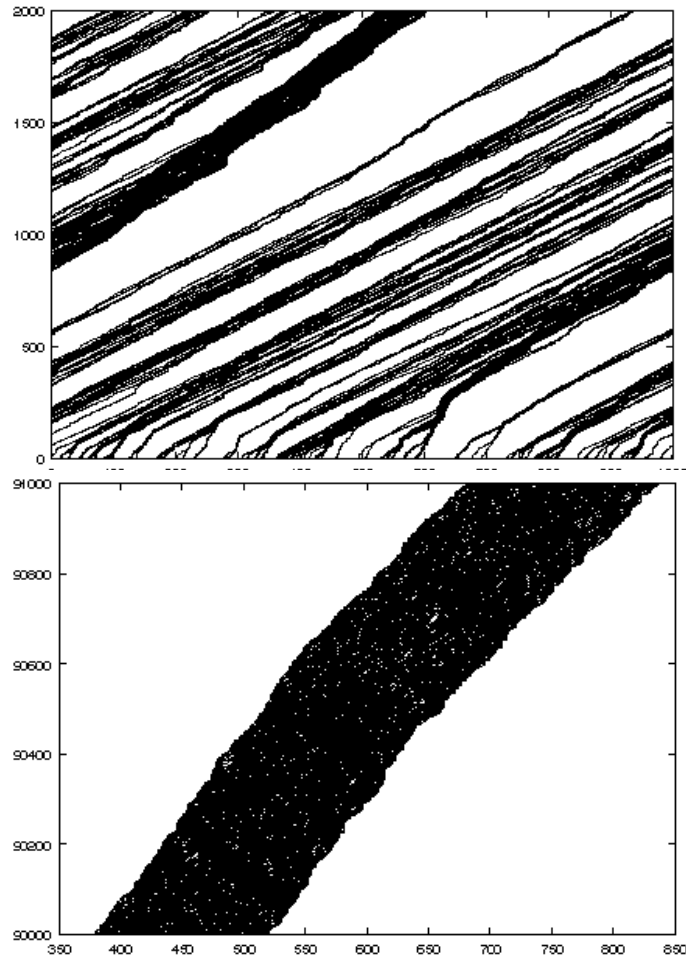
Figure 2: Snapshots of the spatial configurations demonstrating coarsening of the clusters of ants.
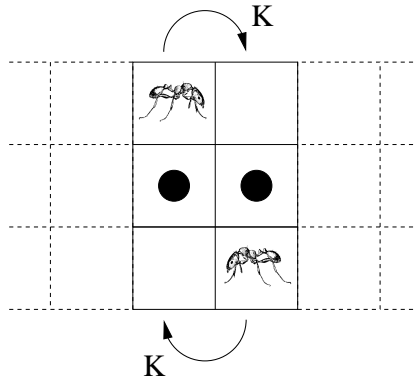
Figure 3: A typical head-on encounter of two oppositely moving ants in the model of *bi-directional* ant-traffic. This is a totally new process which does not have any analog in the model of uni-directional ant-traffic.
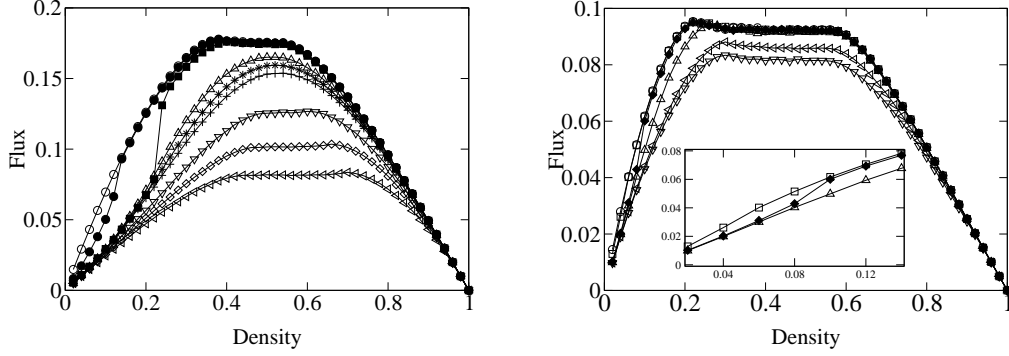
Figure 4: Fundamental diagrams of the model for bi-directional traffic for the cases $q < K < Q$ (left) and $K < q < Q$ (right) for several different values of the pheromone evaporation probability f. **The densities for both directions are identical and therefore only the graphs for one directions are shown.** The parameters in the left graph are $Q = 0.75, q = 0.25$ and $K = 0.5$. The symbols $\circ$, $\bullet$, $\blacksquare$, $\triangle$, $*$, $+$, $\bigtriangledown$, $\diamond$ and $\triangleleft$ correspond, respectively, to $f = 0, 0.0005, 0.005, 0.05, 0.075, 0.10, 0.25, 0.5$ and 1. The parameters in the right graph are $Q = 0.75, q = 0.50$ and $K = 0.25$. The symbols $\circ$, $\square$, $\blacklozenge$, $\triangle$, $\triangleleft$ and $\bigtriangledown$ correspond, respectively, to $f = 0, 0.0005, 0.005, 0.05, 0.5$ and 1. The inset in the right graph is a magnified re-plot of the same data, over a narrow range of density, to emphasize the fact that the unusual trend of variation of flux with density in this case is similar to that observed in the case $q < K < Q$ (left). The lines are merely guides to the eye. In all cases curves plotted with filled symbols exhibit non-monotonic behaviour in the speed-density relation.
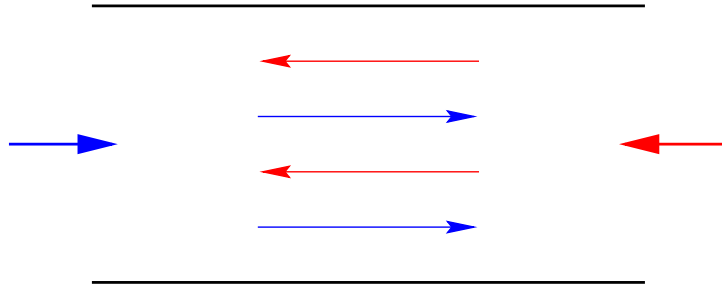

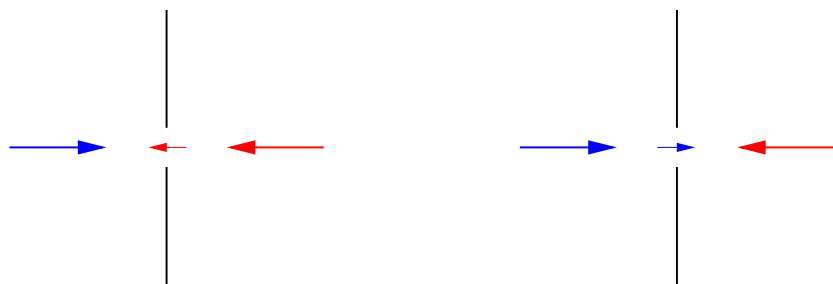Figure 5: Lane formation in counterflow in a narrow corridor.

Figure 6: Oscillations of the flow direction at a door with counterflow.

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